The global trait syndrome for trees with reproductive strategies

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Summary

Understanding trait syndromes can benefit from traits that are closely tied to fitness. In trees, traits are often so weakly tied to fitness that their utility for comparative studies remains uncertain. To address this, we analyze trait syndromes in trees from a perspective that includes fecundity. We gathered 12 million observations of seed production of 775,991 trees in 784 tree species. We tested whether seed production is associated with the leaf economic spectrum, the plant size syndrome, or whether reproduction creates its own, independent dimension related to seed mass and number trade-off. Bringing seed production into trait analysis, while allowing for effect of environment and phylogeny, exposes a number of novel relationships in trees. The most direct connection to fitness, represented by numbers of seeds and production of seed biomass, comes through seed size, which, in turn, associates large seeds with high leaf area, low foliar nitrogen and low SLA, and dense wood. Trees with large leaves, low nutrient demands and low photosynthetic capacity indicated by low foliar nitrogen concentrations and low SLA, that grow slowly to attain dense wood, are being selected for production of large seeds and high investment into seed biomass. Abundant seed shadows are associated with small seeds produced by fast-growing, nutrient-demanding trees with small and cheap leaves. The trait turnover appears to reflect a shift from fast-growing, early successional vegetation with greater dispersal abilities to slower-growing, and stress-tolerant species that recruit in high shade; showing that trees life strategies align along the successional axis globally.

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keywords: fecundity | forest recruitment | functional traits | life history strategies | seed size and number trade-off | size syndrome | leaf economics syndrome

Introduction

Understanding forest diversity can benefit from knowledge of traits that are closely linked to fitness (Adier *et al.*, 2014; Paine *et al.*, 2015; Yang *et al.*, 2018; Kelly *et al.*, 2021). Adaptive evolution operates on variation that affects survival and reproduction. Leaf traits, wood density, and plant height are clearly important for trees, yet their connections to fitness are indirect (Wright *et al.*, 2004; Violle *et al.*, 2007; Chave *et al.*, 2009; Díaz *et al.*, 2016). Large, thin, short-lived leaves with high nitrogen content confer clear advantages in settings where long-lived, highly lignified leaves do not (Shreve, 1925; Field & Mooney, 1986; Reich, 2014). However, interpreting the fitness implications of many traits can require broad extrapolation, such as ecophysiological measurements describing minute-scale responses of leaves, roots, or xylem elements that are integrated with many other responses to determine survival and/or reproduction over the lifetimes of whole plants. While no trait links directly to fitness in trees, many are so weakly tied to fitness that their utility for comparative studies remains uncertain. Seedling recruitment at one site (Rüger *et al.*, 2018, 2020) provides a more direct link to fitness. Given that recruitment varies for each species at each site, species-level reproductive effort could be a valuable extension to trait understanding. The long-term and geographically extensive measurements of tree seed production needed for species-level synthesis is only recently available (Clark *et al.*, 2021; Journé *et al.*, 2022; Qiu *et al.*, 2022; Sharma *et al.*, 2022). With newly available estimates, we re-examine the hypotheses that describe reproduction as part of an omnibus syndrome that explains all traits (e.g., fast-slow) or, alternatively, as a separate axis of variation. Diverging from both extremes, we find that the global link between seed attributes and wood density is more consistent with an adaptive solution that is different from

1

(even orthogonal to) the leaf-economic spectrum.

Principal components analysis (PCA) has been a primary tool for exploring trait variation, contributing to at least three interpretations for forest trees. One view sees reproduction and leaf traits as part of a "fast-slow" continuum of plant strategies (Reich, 2014) (Fig. 1a). That dimension represents the trade-off between resource acquisition and processing, and it could be linked to a growth-survival trade-off (Poorter *et al.*, 2008; Wright *et al.*, 2010; Rüger *et al.*, 2018). Leaves that assimilate carbon quickly, together with low wood density, characterize species that are resource-demanding, grow fast, and die young (Westoby *et al.*, 2002; Moles, 2018). Abundant seed production may offset mortality losses (Muller-Landau, 2010; Reich, 2014). Species with some or all of these traits might dominate early successional stages through effective colonization, and they might not persist under intense competition (Poorter *et al.*, 2008; Wright *et al.*, 2010).
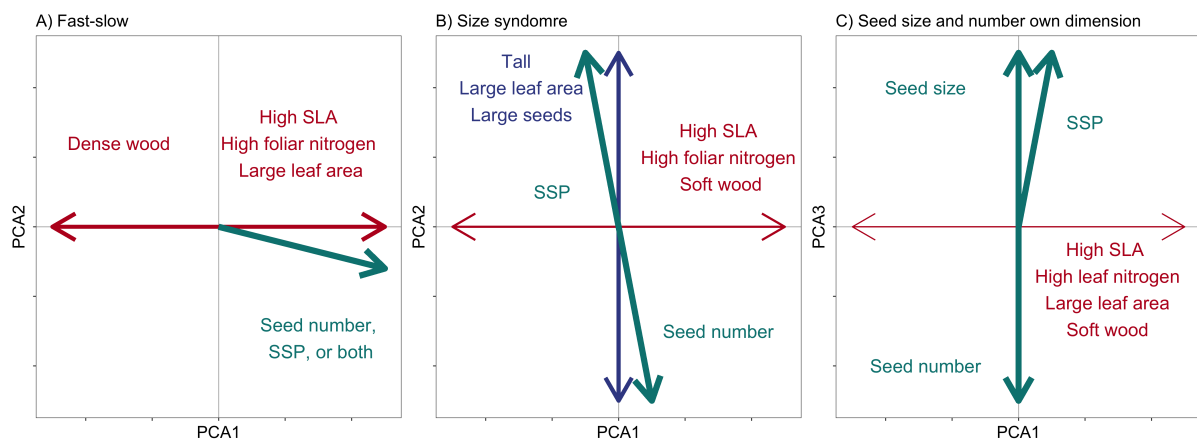

Figure 1: Hypothetical associations between dimensions of plant life strategies represented by functional traits and reproduction. Abundant seed production can be associated with: A) fast life syndrome (slow-fast resource turnover axis); B) plant size syndrome; C) create its own, largely independent axis of seed size-seed number trade-off. Species seed productivity (SSP) is the product of seed number and seed size divided by tree basal area.

Alternatively, the size hypothesis suggests that reproduction is part of a stature-recruitment trade-off (Fig.1b) (Kohyama, 1993; Díaz *et al.*, 2016; Rüger *et al.*, 2018, 2020). According to this hypothesis, large size maximizes canopy performance at the expense of recruitment, and vice versa. The analysis of 282 co-occurring tree species at tropical Barro Colorado Island (BCI) emphasized a leaf-trait axis and a size-recruitment axis (Fig.1b), with species characterized by small stature, small leaves, and small seeds having high recruitment at the BCI (Rüger *et al.*, 2018).

Finally, seed abundance and seed size may represent a third, largely independent, dimension of variation (Fig. 1c), as proposed by the twin-filter (TF) hypothesis (Grime & Pierce, 2012). According to the TF, primary strategies such as fast-slow determine persistence for the climate/habitat norms, while traits involved in episodic events, which might include reproduction, affect fitness independently of the primary strategy (Grime & Pierce, 2012; Pierce *et al.*, 2014). The leaf-height-seed (LHS) scheme of Westoby (1998) hypothesizes that seed size plays a role similar to reproduction in the TF model. In both hypotheses, plants can produce either many or few seeds (TF) or small or large seeds (LHS) independent of other plant traits. All three of the foregoing hypotheses imply an important role for fecundity, and they depend on the assumption that all traits having some connection to fitness. The availability of species-level seed production can lend novel insight to trait analysis due to its close connection to tree fitness.

A limitation of summaries available from PCA comes from the fact that correlations include all the indirect ways that traits could be associated. For example, a seed-size/wood-density correlation could come from a need for high wood density in order to produce large seeds; if true, this would be a direct relationship. Alternatively, both variables might be driven by climate for reasons that do not depend on one another; this is an indirect relationship. Another indirect relationship is represented by phylogenic conservatism; some species groups tend to produce larger seeds or denser wood than others, even as environments that might select for one or both traits change. The correlation structure exposed by PCA does not discriminate between direct (conditional) and indirect (marginal) relationships. If relationships are indirect, then conditional estimates offer the most transparent view of their connections (Seyednasrollah & Clark, 2020).

The Masting Inference and Forecasting (MASTIF) network includes 12 million tree-year observations of seed production on 775,991 trees from 784 tree species from a broad range of biomes (Journé *et al.*, 2022; Qiu *et al.*, 2022). To control for variation within species and, thus, to sharpen our understanding of species differences, we estimate fecundity with an analytical framework that includes trees condition (species, size, shading), habitat (soils), and climate (temperature and moisture deficit), while accommodating dependence between and within trees across years (Clark *et al.*, 2019). The large sample size is important for the notoriously noisy seed production in trees (Kelly *et al.*, 2021), where tree-to-tree and year-to-year variation spans several orders of magnitude (Clark *et al.*, 2004; Journé *et al.*, 2022). The traditional study of trait syndromes with PCA is supplemented here with conditional (direct) relationships between traits using Generalized Joint Attribute Modeling (GJAM) (Clark *et al.*, 2017). Including environment as fixed effects and phylogenetic groups as random effects, GJAM decomposes trait relationships into direct and indirect relationships. By combining seed production with seed size, we show how reproductive traits relate to one another separately and in combination, including on a size basis: the species seed productivity, SSP = seed size × seed number/tree basal area, standardizes for tree size (Qiu *et al.*, 2021). If large seeds confer an advantage in competitive, shaded understories, while many, small seeds allow colonization of distant sites, then species seed productivity (SSP) provides a direct link to reproduction.

Results

Across the 784 species in this analysis, dominant sources of variation derive from foliar traits and seed/wood density. In the principal components analysis (PCA) of our data that includes mean annual SSP (species seed productivity as seed biomass per m^2 tree basal area), 54.2% of variation is concentrated in two principal components of equal importance (Fig. 2A). PCA1 is associated with leaf traits. At one end are species with thin, large, acquisitive leaves (large SLA, high area, high foliar nitrogen), including heaven lotus (*Gustavia superba*), Panama tree (*Sterculia apetala*), pawpaw (*Asimina triloba*), and eastern walnut (*Juglans nigra*). At the other end are species with low SLA, low foliar nitrogen, and low leaf area, including evergreen conifers like giant sequoia (*Sequoiadendron giganteum*), California redwood (*Sequoia sempervirens*), monkey puzzle (*Araucaria araucana*), Fraser fir (*Abies fraseri*), and white cedar (*Thuja occidentalis*). PCA2 is dominated by seed size, SSP, and wood density. Large seeds are associated with high SSP, because seed size has a larger effect on SSP than does seed numbers (Qiu *et al.*, 2022). Dense wood is associated with both variables, with examples including African crabwood (*Carapa procera*) and Fagales like chestnuts (*Castanea*) and oaks (*Quercus*). At the opposite end with low-density wood and small seeds are willows (*Salix*), fuchsia (*Fuchsia excorticata*), and trumpet tree (*Cecropia obtusa*). Tree height is weakly associated with foliar attributes: small trees tend to have large, thin leaves.

A second PCA in which SSP is replaced with seed number (seeds per m^2 tree basal area, rather than seed mass per m^2 tree basal area) yields similar results (Fig. S2). As with the PCA using SSP (fig. 2A), the first axis of this second PCA is associated with foliar traits with no contributions from seed numbers. The second PCA axis separates species according to seed size, seed number, and wood density. Tree height is again weakly associated foliar attributes but also with reproduction: small trees tend to produce small seeds in large numbers (Fig. S2).
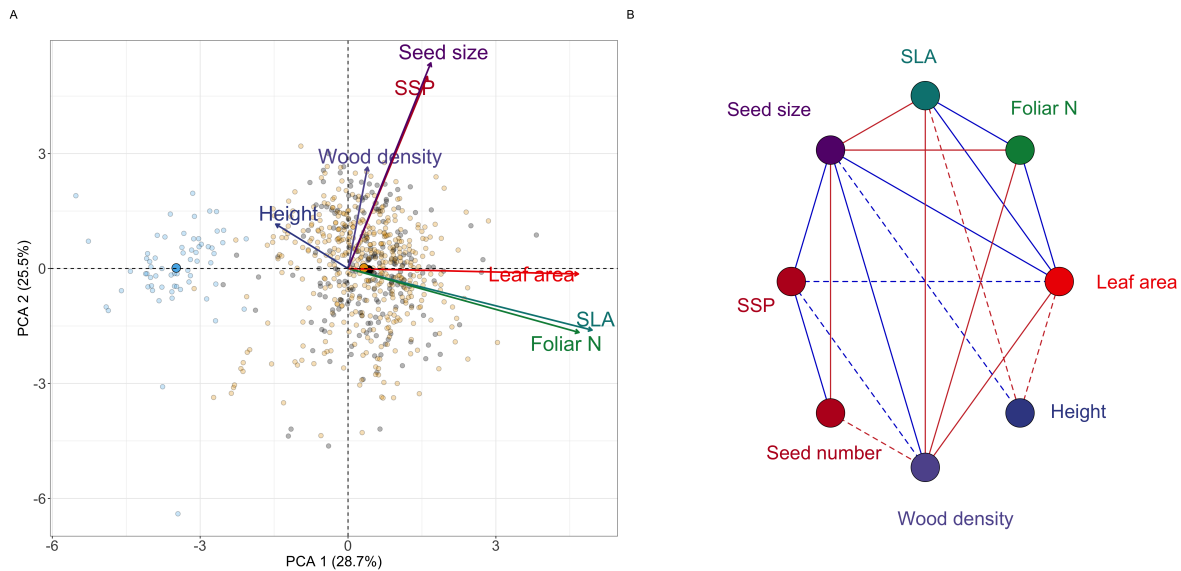

Figure 2: Fecundity on the global spectrum of tree form. A) Biplot; arrows length indicates the loading of each considered functional trait onto the first two PCA axes. Points represent the position of species, coded blue for needle, black for broad-deciduous, and yellow for broad evergreen leaf habit. B) Summary of GJAM coefficients presented at Fig. 3. Significant associations between traits are highlighted by lines, coded red for negative and blue for positive relationship. Dashed lines highlight associations that are significant only in model without phylogenetical control (see Fig. S3). Extended PCA plots are available in supplement Fig. S2. SSP stands for species seed production and is the product of seed size × seed number. Both SSP and seed number are standardized to a tree basal area. Traits are summarized in Table 1.

Conditional associations that allow for the effects of environmental conditions and taxonomic relatedness show that seed size is positively related to SSP and negatively related to seed number (Fig. 2B). The solid lines in Fig. 2B are different from zero in Figure 3, whereas dashed highlight associations that are significant only in model without phylogenetical control. Nutrient-demanding species with high foliar nitrogen concentrations and high SLA produce small seeds, a relationship that is not apparent in PCA. Large seeds are produced by trees with dense wood, low seed number, high leaf area, low foliar N, and low SLA (Fig. 3B-G). Relationships between high SSP and dense wood and between large seeds and tree height are suggested by PCA (Fig. 2A), but these relationships are not significant after accounting for environment and phylogeny (Fig. 2B). Although the links between wood density and foliar traits are significant, they are weaker than the relationships of wood density with seed attributes (Fig. 3D).

Discussion

Across 784 species in our sample spanning from tropical to boreal environments, the introduction of tree fecundity brings a direct connection of trait syndromes to fitness. Seed production makes a dominant contribution to trait syndromes in trees, but one that is not strictly consistent with
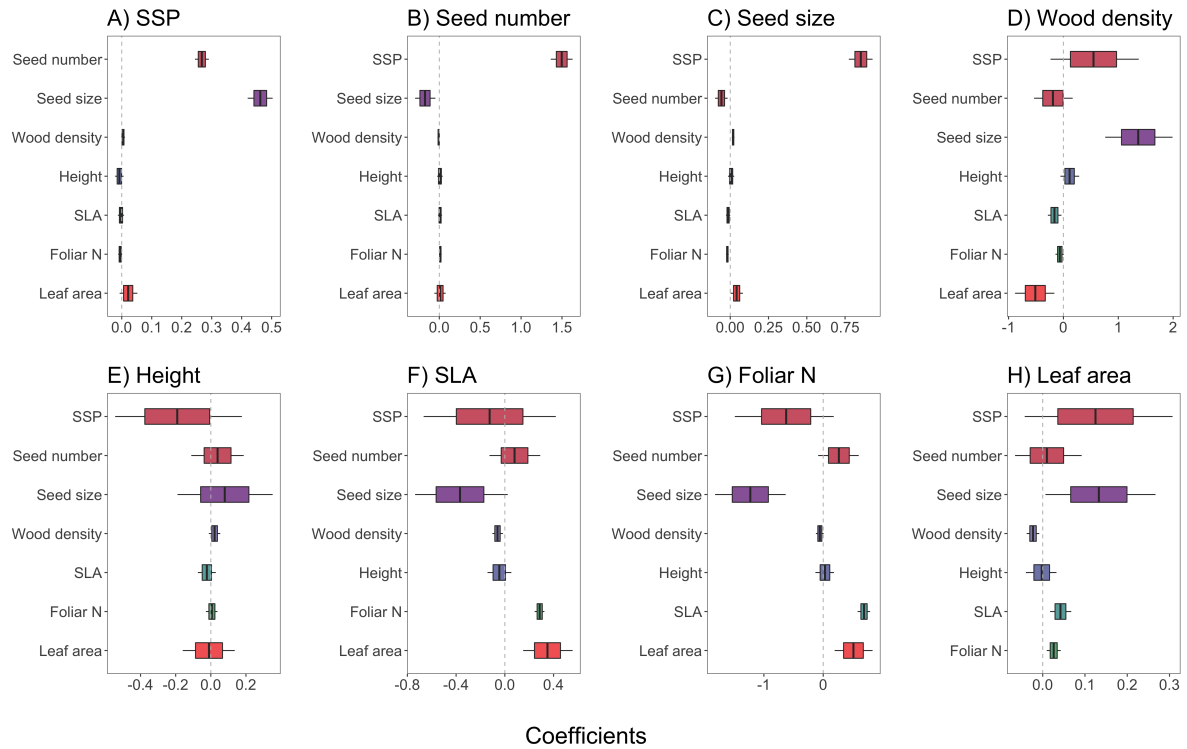
Figure 3: Conditional relationships between traits after accounting for climate and shared ancestry. Marginal posterior distributions are shown as boxes that contain median vertical lines and are bounded by 68% credible intervals (CI), with 95% CI whiskers. Fig. 2 summarizes the significant relationships. See Fig. S3 for conditional relationships derived from GJAM without the phylogenetic control. SSP stands for species seed production and is the product of seed size × seed number. Both SSP and seed number are standardized to a tree basal area. Traits are summarized in Table 1.

fast-slow or stature trade-offs. The traits most directly connected to fitness include numbers of seeds and SSP (seed mass for a given tree size). Because seed size is weakly associated with high leaf area, low foliar nitrogen, low SLA, and dense wood, there is a weak, indirect link of these traits to SSP, but not to seed number. Fast strategies, as captured by leaf traits, were not coupled with abundant seed production, even though nutrient demanding trees show a tendency to produce small seeds. Reproduction (seed size and number) was also not associated with tree height as in the stature-recruitment hypothesis at a tropical BCI (Rüger *et al.*, 2018, 2020). Across all species and sites in this study, trees with dense wood, large leaves, and low nutrient demands produce large but few seeds. These species invest heavily in seed biomass, as indicated by high SSP. In contrast, high seed number is associated with small seeds, most common in species with low-density wood, low leaf area, high foliar N, and high SLA.

Trait syndromes identified here are consistent with traditional trait concepts, including turnover through succession (Bazzaz, 1979; Falster & Westoby, 2005; Wilfahrt *et al.*, 2014). Production of abundant, small seeds increases recruitment in distant, disturbed habitats (Muller-Landau, 2010). The *r* strategy of the *r-K* spectrum is associated with fast growth and high nutrient requirements (Bazzaz, 1979; Huston & Smith, 1987; Henery & Westoby, 2001; Muller-Landau *et al.*, 2008). By including reproduction, our analysis indicates that the traditional *r* strategy, which might include low-density wood that often comes with fast growth (Chave *et al.*, 2009), includes production of small seeds. High foliar nitrogen and cheap leaf construction (high SLA) agrees with high photosynthetic rates (Reich & Oleksyn, 2004; Reich, 2014; Moles, 2018). On the *K* side are species with dense wood and slow growth (Westoby, 1998; Poorter

5

et al., 2005). Low foliar nitrogen and low SLA can align with low foliar Rubisco content, low photosynthetic capacity, and, thus, low maintenance respiration in low light (Reich et al., 1998; Poorter, 2015; Moles, 2018). Species with such conservative leaves are also selected for large seeds needed for seedling establishment in shade, at the expense of the many small seeds that would promote colonization of distant sites (Westoby et al., 2002; Muller-Landau, 2010). High SSP further suggests selection for proportionally high reproductive investment per individual to maintain populations in low light conditions (Kohyama et al., 2003; Falster & Westoby, 2005).

Estimates of reproductive investment for a given tree size, or SSP, enrich the interpretation of plant reproductive strategies beyond the insights that come from seed size alone (Westoby et al., 2002; Muller-Landau, 2010; Lebrija-Trejos et al., 2016). Production of small, copious seeds increases the number of recruitment opportunities at the cost of limited investment per individual seed. Small seeds can mean low tolerance of abiotic stress and limited resources in competitive sites (Westoby et al., 2002; Tilman, 1994; Fricke et al., 2019). Conversely, large seeds come with a cost of producing fewer of them (Henery & Westoby, 2001; Muller-Landau et al., 2008; Fricke et al., 2019). That trade-off means that small-seeded species produce more germinants per unit of reproductive mass, while large-seeded species should produce better performing seedlings in smaller numbers (Fricke et al., 2019; Muller-Landau et al., 2008). However, the size-numbers trade-off is not 1:1 (Qiu et al., 2022). Instead, species that produce large seeds more than compensate (on a mass basis) for fewer of them, resulting in higher SSP (seed mass per tree basal area (Qiu et al., 2022)). The size-numbers trade-off will differ for each species in each setting. Nevertheless, the higher seed biomass investment in high-SSP species means that simultaneous inclusion of seed size and number provides the most accurate link to reproductive potential.

The divergent results from this study and those suggesting a stature-recruitment trade-off at a tropical site (Rüger et al., 2018, 2020; Guillemot et al., 2022) are not necessarily in conflict. The within-site covariation in traits, where short trees might be associated with small seeds and leaves in the shaded understory (Rüger et al., 2018), need not predict with among-site, species level difference, which average over environments for a each species at many sites. At the species level, fecundity is largely independent of tree size and more closely aligned wood density and several foliar traits.

Anticipating individual and combined effects of global change pressures on future forests requires understanding vulnerability not only of mature trees, but also of fecundity and re-cruitment (McDowell et al., 2020; Sharma et al., 2022; Clark et al., 2021; Bogdziewicz, 2022; Hanbury-Brown et al., 2022). Earth system models currently assume that reproductive alloca-tion is indifferent among plant functional types (Scholze et al., 2006; Hanbury-Brown et al., 2022). There is area and promise for improvement as shown by a recent study at the BCI that accurately predicted forest succession by replacing the hyperdiversity of tropical forest with just two trait axes associated with fast-slow and size dimensions (Rüger et al., 2020). Globally, significant links exist between fecundity and trait syndromes that broadly reflect turnover of trees life strategies across successions time. However, many of these trait relationships appear to weak to be useful predictors of fecundity in the Earth system models. Instead, easily measurable seed mass had strong links to SSP and seed number, and can form a first basis of fecundity prediction across global forests.

Acknowledgments

Methods

Trait relationships A data set, including one that might be assembled from meta-analysis, contains species that are characterized by traits and sample locations, each with its own environmental setting. PCA summarizes correlation in the joint distribution of traits, written in bracket notation as $[\mathbf{T}] = [T_1, \ldots, T_M]$. If the relationship between traits depends on phylogeny, summarized by phylogenetic groups $P_{g=1\ldots G}$ (taxonomic, e.g., genus or family), and on the environment X, then there is a joint distribution $[\mathbf{T}, P, X]$. The indirect environment and phylogeny effects may dominate the relationships between some or many traits. An alternative approach uses the conditional distribution,

$$[\mathbf{T}|P, X] = \frac{[\mathbf{T}, P, X]}{[P, X]} \tag{1}$$

where the distribution of groups and environments $[P, X]$ is that which occurs in the data set.

To determine trait relationships we fit a joint model to the conditional distribution $[\mathbf{T}|P, X]$, which provides estimates of the of phylogeny as random groups $\mathbf{g}[s]$, $g = 1, \ldots, M$ for species s and X as a $Q \times M$ matrix of coefficients $\mathbf{B}$. We then decompose the distribution into (conditional) effects of other traits and the environment. The effect of trait m on the remaining $-m$ traits is the conditional distribution $[\mathbf{T}_{-m}|T_m, P, X]$. Using the fitted model in GJAM (see below), we decompose the conditional effect of m on other traits as,

$$E(\mathbf{T}_{-m}|T_m, P, X) = E(\mathbf{T}_{-m}|T_m) + E(\mathbf{T}_{-m}|P, X) \tag{2}$$

The first term is a conditional influence of m as distinct from (P, X).

Fecundity data and MASTIF model Seed production in perennial plants suffers from extreme signal-to-noise problem, created by orders of magnitude variation from year to year and tree to tree (Pesendorfer *et al.*, 2021; Pearse *et al.*, 2020; Clark *et al.*, 2004) that can can bury any trends (Clark *et al.*, 2021). Autoregression models assume a fixed periodicity, but mast intervals are not fixed (Shibata *et al.*, 2020; Pesendorfer *et al.*, 2020). There are as many time series as there are trees that must be modeled together because there is dependence created by among-trees synchrony in masting variation (Crone *et al.*, 2011; Bogdziewicz *et al.*, 2021). Masting patterns are further complicated by spatio-temporal variation in habitat and climate (Pesendorfer *et al.*, 2021; Pearse *et al.*, 2020). The many sources of variation means that estimation of trees fecundity can only be achieved from broad coverage and large sample sizes, while accounting

for individual tree condition, local habitat, and climate (Clark *et al.*, 2021; Qiu *et al.*, 2021; Sharma *et al.*, 2022). This is here achieved with the MASTIF model (Clark *et al.*, 2019).

The MASTIF model and data from the Masting Inference and Forecasting (MASTIF) network are summarized here, and extensively described in recent papers (Clark *et al.*, 2019, 2021; Qiu *et al.*, 2021; Sharma *et al.*, 2022). The tree-year observations in the network comes from seed traps and from crop counts. Data include longitudinal (repeated) observations on individual trees (99%) and opportunistic observations that come through the iNaturalist project (Clark *et al.*, 2019). Seed trap data consist of numbers of seeds that accumulate annually in mapped seed traps on forest inventory plots. A fitted dispersal kernel relates seed counts to mapped trees, accounting for uncertainty in seed transport and Poisson seed counts (Clark *et al.*, 2019). Crop counts include counts of reproductive structures with estimates of the fraction of the crop observed, and beta-binomial distribution accounts for uncertainty in the crop-fraction estimates (Clark *et al.*, 2019). This study includes 12,008,722 tree-years from North America, South and Central America, Europe, Africa, Asia, and Oceania, which is gathered over 5,115 plots and 787,444 trees (Fig. 4). Unlike meta-analysis, the MASTIF model jointly estimate trees fecundity based on all the observations; the SN and SSP used in the PCA analysis are calculated based on 297,690 mature individuals and 3,730,381 tree-years. The list of species included in the analysis is given in the Online Supplement as a csv file.
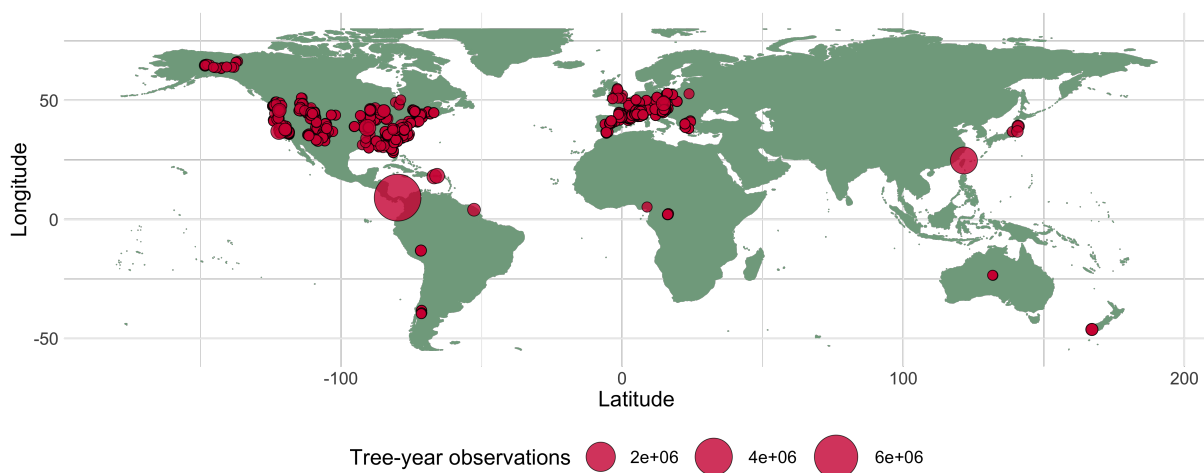
Figure 4: Map of raw data used to estimate trees fecundity with the MASTIF model.

The MASTIF model, detailed in Clark *et al.* (2019), is a dynamic biophysical model for year-to-year and tree-to-tree seed production. The MASTIF model is Bayesian hierarchical, state–space model that allows for conditional independence in crop-count and seed-trap data through latent states. The model estimates seed production with conditional fecundity, which depends on a probability that the tree is sexually mature, tree size, shading, local climate, and soil conditions. Random effects on individual and year allow for wide variation between trees and over time that are typical of seed production. The posterior covariance between trees and years can take any form, avoiding assumptions of standard time-series models, important due to the quasiperiodic variation in time and varying levels of synchronicity between individual trees. Model structure and methodology was implemented with R, version 4.0 (R Core Team, 2020) and the R package Mast Inference and Forecasting (MASTIF) (Clark *et al.*, 2019).

Fecundity at the species level   We estimated species investment into seed production using two metrics, both scaled to the tree basal area: annual seed number (SN), and species seed productivity (SSP), which can be summarized as annual seed biomass investment (seed number × seed mass) (Qiu *et al.*, 2022). Estimation of both SN and SSP starts with the estimation of individual tree mean seed production that depends on each tree location that accounts for effects of the environment and includes uncertainty for each year. Individual trees seed production over a species is then summarized as SN or SSP. Tree-level estimate of seed production, i.e., individual seed production (ISP), is the product of mass per seed m_s and seeds per tree basal area per year. Calculation of ISP combines posterior mean values with their uncertainties, as an expectation over the variations across years:

$$\text{ISP}_{ijs} = \frac{m_s}{b_{ij}} \times \frac{\sum_t w_{ijs,t} \hat{f}_{ijs,t}}{\sum_t w_{ijs,t}} \tag{3}$$

where m_s is seed mass (g), b_{ij} is basal area (m^2), and weight $w_{ijs,t}$ is the inverse of the coefficient of variation (CV),

$$w_{ijs,t} = CV_{ijs,t}^{-1} = \hat{f}_{ijs,t}/s_{ijs,t} \tag{4}$$

$s_{ijs,t}$ is the standard error of the estimate. The CV^{-1} is used instead of the inverse of variance, because the mean tends to scale with variance. Low values for $\hat{f}_{ijs,t}$ are noisy and less important than high values, which are emphasized by the CV. We quantify ISP as the mass of a tree's seed production relative to its basal area to standardize for tree size (intermediate trees produce more seeds than smaller ones Qiu *et al.* (2021)). All estimates are time averages across annual estimates, so we hereafter omit yr^{-1} from dimensions. Therefore, ISP has the units of g/m^2.

Species seed production (SSP) comes from expectation of all ISP for a given species *s*:

$$\text{SSP}_s = \frac{\sum_{ij} w_{ijs} \text{ISP}_{ijs}}{\sum_{ij} w_{ijs}} \tag{5}$$

where w_{ijs} is defined the same way as $w_{ijs,t}$, i.e., root mean predictive variance divided by the mean ISP for tree ijs. Analyses of SSP are done on the proportionate (log) scale to avoid dominance of results by the few species that produce the highest seed production. Visualizations are based on $\log_{10}$ to facilitate interpretation of scales in results. SN is estimated following the same steps, but the calculations omits seed mass (g).

Functional traits   We selected six functional plant traits previously shown to well capture plant life strategies (Díaz *et al.*, 2016; Carmona *et al.*, 2021) (Table 1): plant height (measured in m), leaf area (measured in mm^2), specific leaf area (SLA; measured in mm^2/mg; the inverse of leaf mass per area), leaf nitrogen concentration (measured in mg/g), wood density (measured in g/m^3) and seed mass (measured in mg). The data was obtained from primary sources and supplemented with publicly available data from the latest version of the TRY Plant Trait Database TRY Plant Trait Database (Kattge *et al.*, 2020) extracted from the Carmona *et al.* (2021). Missing values for the six traits were filled with genus-level means. Bivariate relationships are summarized at Fig. S4).

Generalized joint attribute modeling   To incorporate the effects of environment and phylogeny on the distribution of traits, we use GJAM to account for the different variable types represented by each trait (Clark *et al.*, 2016). Trait variable types are given in Table (Table 1). Environmental covariates include soil fertility (Cation Exchange Capacity), mean annual

Table 1: Summary of traits used in the analysis.

Trait	Units
Species seed production (SSP)	g/m^2
Seed number	$seeds/m^2$
Seed size	mg
Height	m
Wood density	g/m^3
Leaf area	mm^2
Leaf nitrogen	mg/g
SLA	mm^2/mg

temperature, and annual moisture deficit (difference between potential evapotranspiration and precipitation) averaged at the species level for the MASTIF data set. GJAM allowed us to accommodate the dependence between traits and phylogeny as random groups.

To partition the expected effects a trait on others (eq. (2)), we start with the joint distribution of M traits from a species s fitted with GJAM,

$$[\mathbf{T}_s|P, X] = MVN_M(\mathbf{T}_s|\mathbf{B}'\mathbf{x}_s + \mathbf{g}[s], \Sigma)$$
$$\mathbf{g} \sim MVN(\mathbf{0}, \Omega) \tag{6}$$

(Clark *et al.*, 2016), where $\mathbf{g}[s]$ is a random vector for the phylogenetic group to which s belongs, and Ω is the $M \times M$ covariance between traits taken over phylogenetic groups. With this fitted model, we consider the effects of trait m on all other traits, organized in the vector $[\mathbf{T}] = [\mathbf{T}_{-m}, T_m]$. We can partition the mean and covariance as

$$\mathbf{B} = \begin{pmatrix} \mathbf{B}_{-m} \\ \mathbf{B}_m \end{pmatrix} \tag{7}$$

where $\mathbf{B}_m$ holds column m and $\mathbf{B}_{-m}$ holds the other $M - 1$ columns of $\mathbf{B}$. The covariance matrix is also partitioned as

$$\Sigma = \begin{pmatrix} \Sigma_{-m,-m} & \Sigma_{-m,m} \\ \Sigma_{m,-m} & \Sigma_{m,m} \end{pmatrix} \tag{8}$$

This joint distribution allows us to isolate the contributions of trait m as a conditional distribution. Substracting the random effect for species s gives the trait vector $\tilde{\mathbf{T}}_s = \mathbf{T}_s - \mathbf{g}[s]$. Then

$$\tilde{\mathbf{T}}_{-m,s}|T_{m,s} \sim MVN(\boldsymbol{\mu}_{-m,s}, \mathbf{P}) \tag{9}$$
$$\boldsymbol{\mu}_{-m,s} = \mathbf{B}_{-m}\mathbf{x}_s + \mathbf{A}(T_{m,s} - \mathbf{B}_m\mathbf{x}_s)$$
$$= \mathbf{C}\mathbf{x}_s + \mathbf{A}T_{m,s} \tag{10}$$
$$\mathbf{P} = \Sigma_{-m,-m} - \mathbf{A}\Sigma_{m,-m} \tag{11}$$

There are now two sets of coefficients, a length $M - 1$ vector for effects of m, $\mathbf{A} = \Sigma_{-m,m}\Sigma_{m,m}^{-1}$, and another $M - 1 \times Q$ matrix for effects of $\mathbf{x}$, $\mathbf{C} = \mathbf{B}_m - \mathbf{A}\mathbf{B}_m$. The elements of matrix $\mathbf{A}$ are arrows in figure fig. 2. Matrix $\mathbf{A}$ were obtained with the `conditionalParameters` function in the GJAM package. GJAM fitting is open-access with R package `GJAM` on CRAN.

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Supplementary material

This Supplement provides additional data summaries as tables and figures. Full summaries of
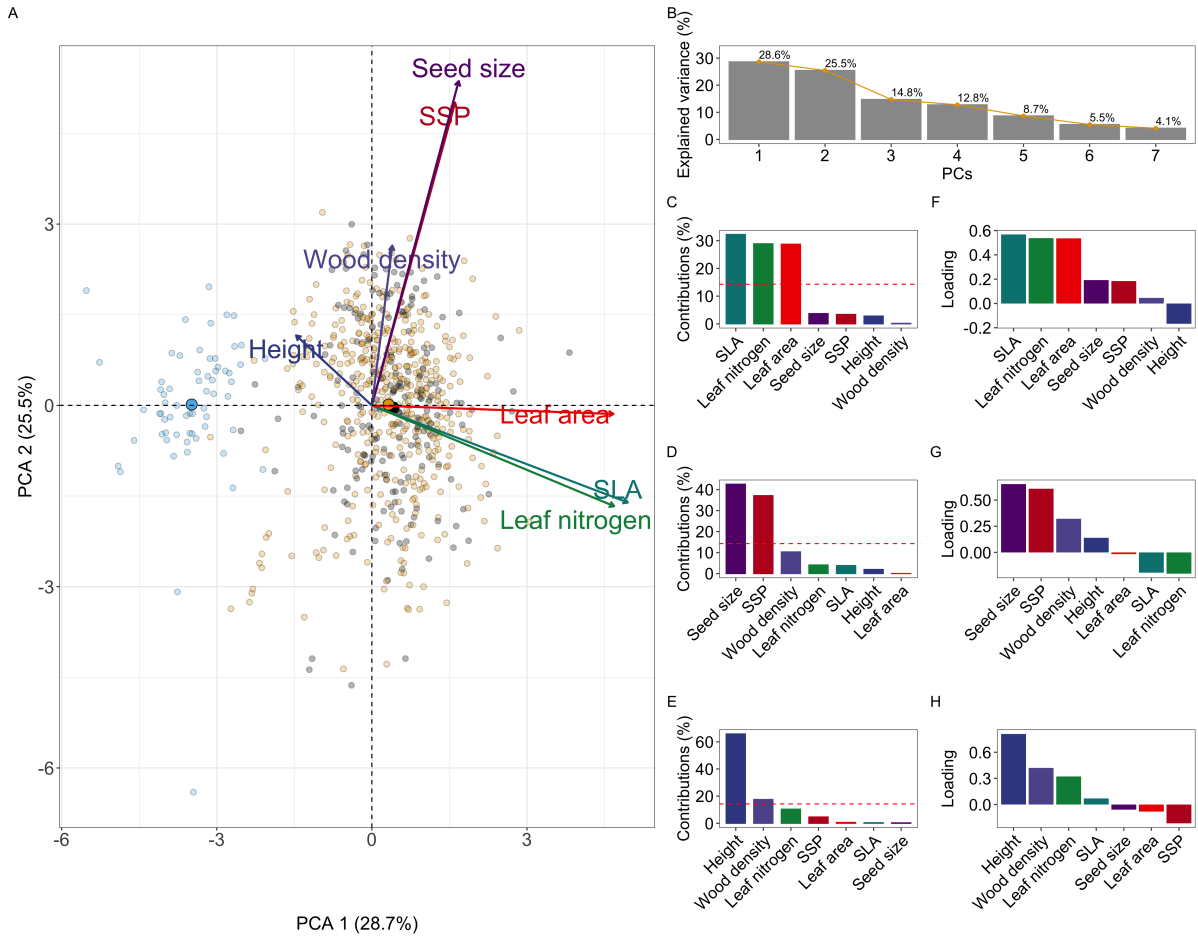the MASTIF network are available these links for sites and species.

Figure S1: PCA as presented on Fig. 2 extended with contributions and loadings of the three axes that explained
the most variance. A) Species seed productivity (SSP) on the global spectrum of tree form. Arrow length indicates
the loading of each considered functional trait onto PCA axes. Points represent the position of species. B) Explained
variance for each principal component. Bar plots of the contribution (C,D,E) and loading (F,G,H) of each trait to
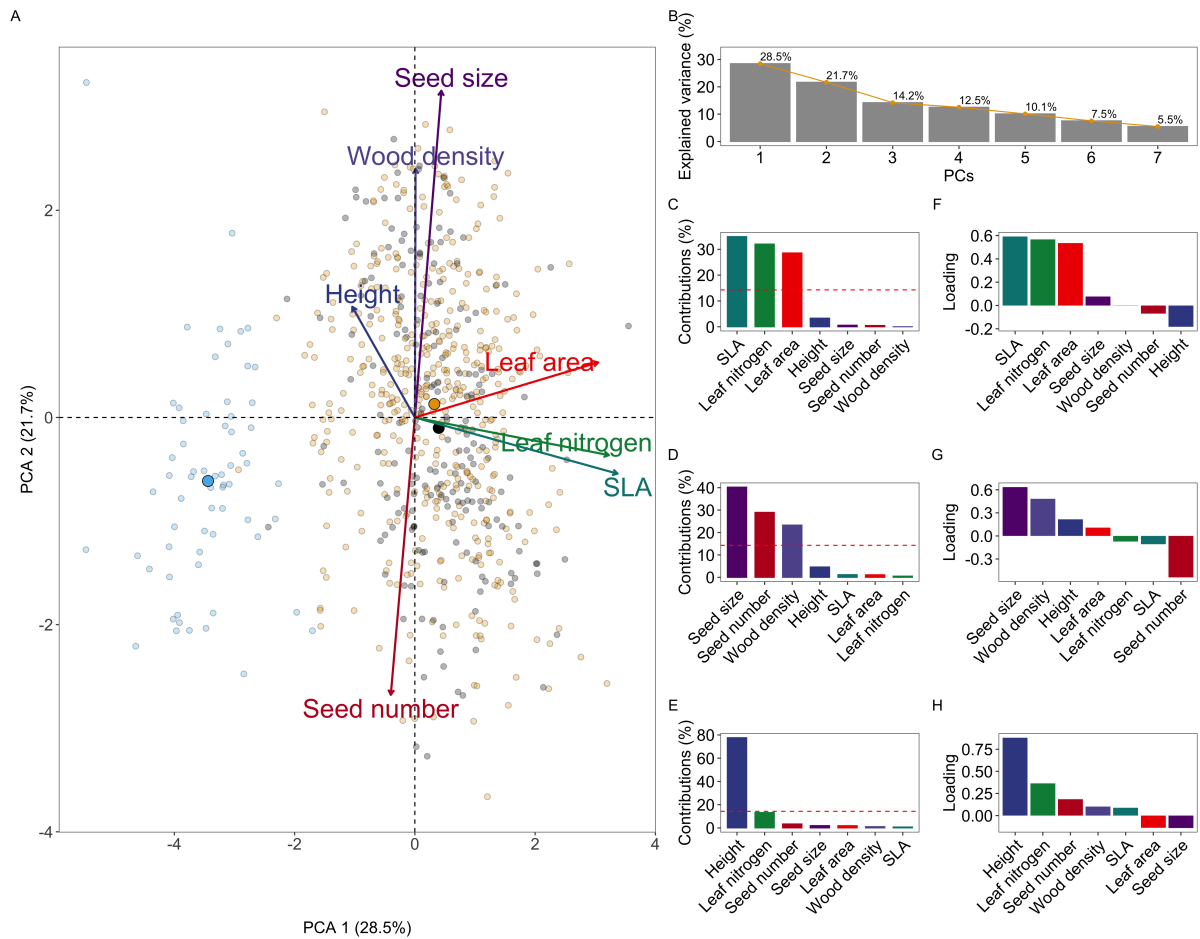each principal component. Large point shows the mean position for each group .

Figure S2: A) Species fecundity (seed number) on the global spectrum of tree form. Arrow length indicates the loading of each considered functional trait onto PCA axes. Points represent the position of species. B) Explained variance for each principal component. Bar plots of the contribution (C,D,E) and loading (F,G,H) of each trait to each principal component. Large point shows the mean position for each group .
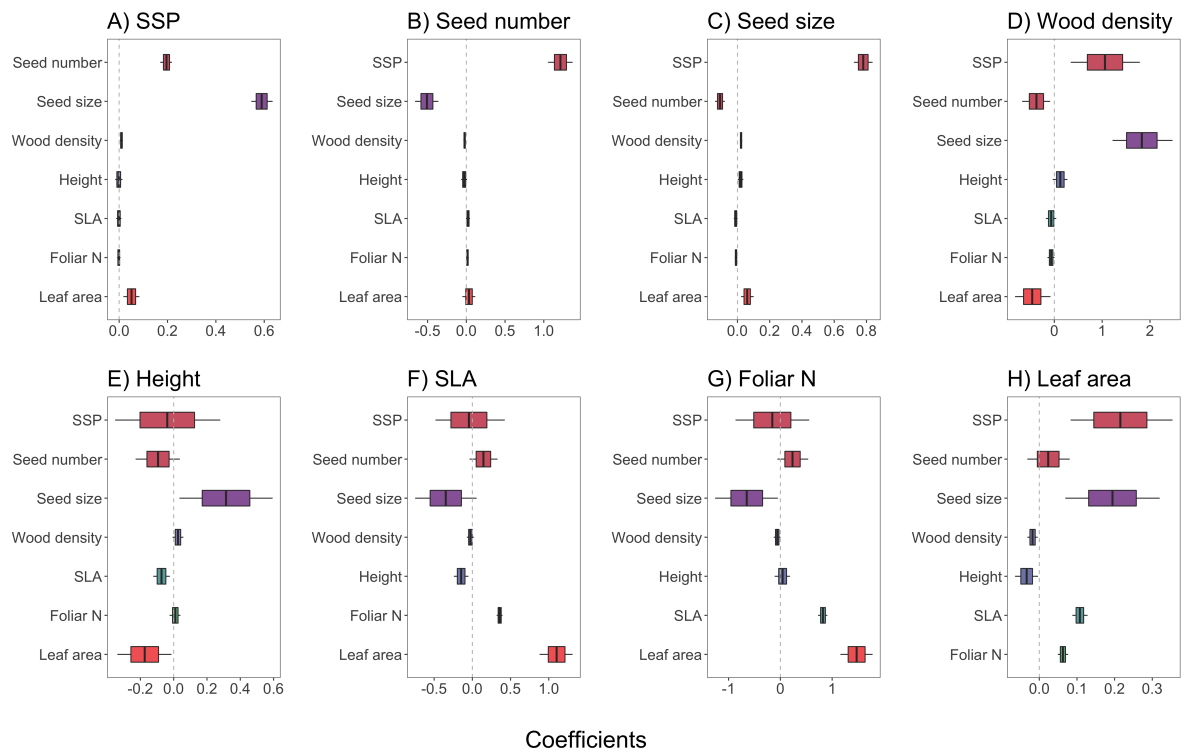
16

Figure S3: Conditional relationships between traits after accounting for climate but not shared ancestry. Marginal posterior distributions are shown as boxes that contain median vertical lines and are bounded by 68% credible intervals (CI), with 95% CI whiskers. Fig. 2 summarizes the significant relationships.
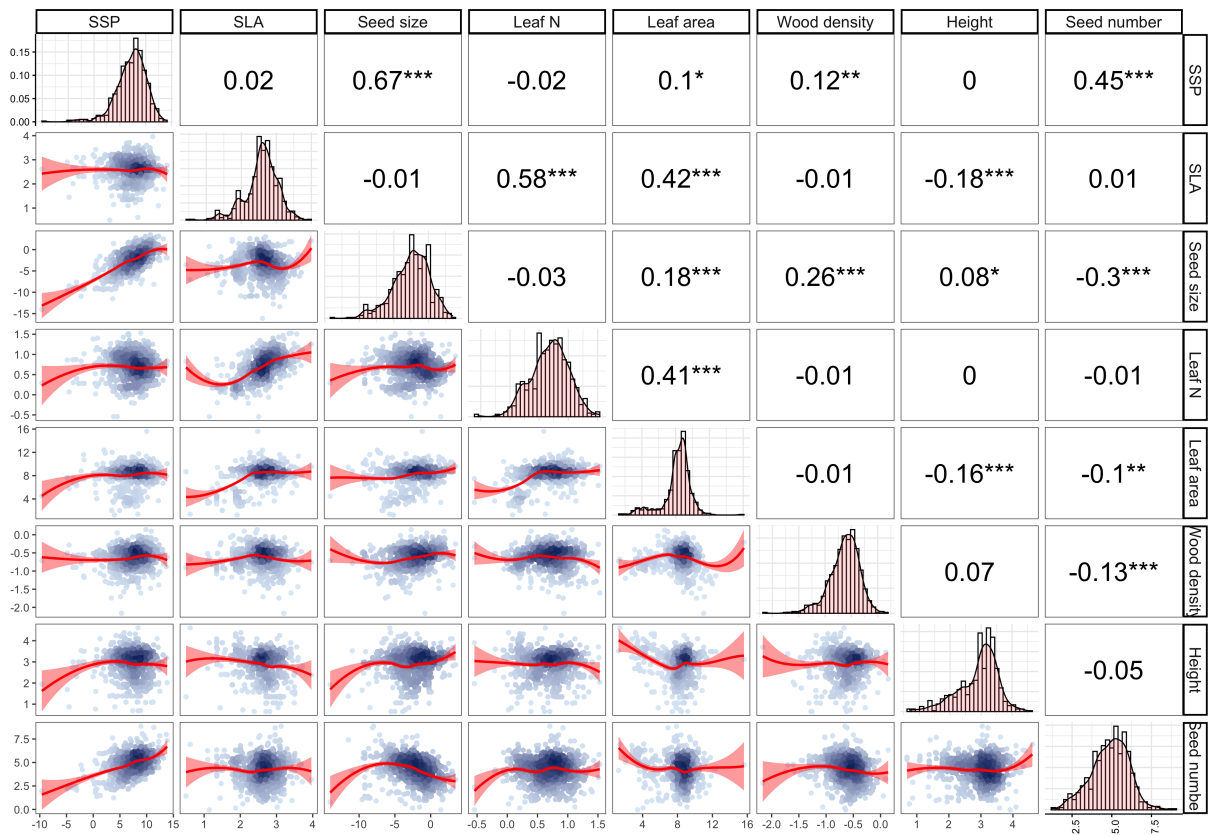
Figure S4: Summary of bivariate relationships between considered traits. Points are species, lines are loess regression and associated 95% CI. Coefficients are Pearson correlations. Traits are log-transformed.